STUDIES ON THE FIREFLY

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STUDIES ON THE FIREFLY. I. THE EFFECTS OF LIGHT AND OTHER AGENTS ON FLASHING IN PHOTINUS PYRALIS, WITH SPECIAL REFERENCE TO PERIODICITY AND DIURNAL RHYTHM[1]

(Nine figures)

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IT IS well known that in nature the males of the firefly *Photinus pyralis* ordinarily remain quiescent during the bright light of day and do not flash; that in the dim light of dusk, at about 7:00 P.M., they become active and fly about and flash; and that at about 9:00 P.M. with the onset of darkness, they become quiescent again and remain so until the next evening.

Mast (1912) discussed in detail the time of appearance ("first glow") of *P. pyralis* in the evening. He observed that "the time of the day the first glow appeared was surprisingly constant"; and he concluded, "It appears that the activity of these creatures is a periodic phenomenon to a considerable extent independent of immediate environmental changes."

Allard (1931) made extensive observations on the same species and concluded that flashing begins earlier on cloudy than on clear days, and that the time at which flashing begins gradually becomes earlier as the season progresses.

Rau (1932) maintained that in the darkest and lightest areas near his laboratory there was a consistent difference of from 25 to 40 minutes in the time at which the first flash occurred in this species. He also observed on one afternoon that the fireflies flashed when it became very dark just before a thunderstorm.[2] He concluded that "these creatures are stimulated to action by definite light conditions and not by a blind rhythmic impulse from within."

Mast noted that "low temperature . . . . seems to retard their appearance." Allard made a large number of records of the temperature at the time of the first appearance of the fireflies in the evening but did not draw any conclusion.

There are, then, two antagonistic views with reference to the influence of light on flashing in the firefly. Mast, on the one hand, is inclined to minimize the effects of light and to emphasize internal factors; whereas Allard and Rau, particularly the latter, hold that light intensity and time of appearance are closely related and that internal factors are not involved.

The purpose of this investigation is to clarify the disputed views presented above and to ascertain more precisely the relations between various environmental factors (particularly light) and flashing in the firefly. The results presented were obtained entirely from work done on males of the firefly *Photinus pyralis* Linn. at Baltimore, Md.

[1] This work represents part of a dissertation submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy in the Johns Hopkins University. It was performed under the direction of Professor S. O. Mast, whose generous advice and assistance the author is happy to acknowledge.

[2] Observed also by Laurent (*Entomological News*, 25 [1914], 334) and by the present writer.

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OBSERVATIONS IN THE FIELD

The writer attempted to put the field observations on a more accurate basis by measuring, on a considerable number of evenings, both the light and the temperature at the time and the place of the first flash observed. The main results of these observations are presented in Table I. This table shows that all of the factors recorded varied somewhat, but always within fairly narrow limits. Comparison of observation 6 with 7, and 15 with

TABLE I

RELATION BETWEEN TEMPERATURE, LIGHT INTENSITY, AND THE TIME OF FIRST FLASH

The observations are arranged in the order of increasing light intensity. The lines drawn through the fourth column separate groups of light intensities which were averaged together and plotted against the averages of the corresponding temperatures (col. 5) in Figure 1.

Observation	Date (July, 1933)	Weather	Light Intensity (Meter-Candles)	Temperature (Degrees Centigrade)	Time of First Flash (P.M., E.S.T.)
1	27	Hazy	26	21.1	7:15
2	19	Hazy	35	23.9	7:10
3	14	Cloudy	40	17.8	7:28
4	11	Hazy	41	22.0	7:20
5	28	Cloudy	45	22.3	7:01
6	5	Clear	55	23.3	7:22
7	10	Overcast	55	23.3	6:40
8	7	Clear	55	20.5	7:24
9	16	Clear	56	25.5	7:08
10	13	Hazy	70	21.7	7:10
11	20	Hazy	75	26.7	6:58
12	17	Hazy	79	25.0	7:08
13	25	Overcast	84	26.7	6:59
14	18	Hazy	87	24.4	7:06
15	12	Clear	100	22.3	7:06
16	15	Overcast	100	22.3	6:45
17	6	Clear	100	25.5	7:16
18	21	Clear	110	26.7	7:10
19	24	Hazy	130	25.5	7:01
20	8	Cloudy	140	26.7	7:10

16, indicates that (other conditions being equal) the fireflies tend to begin to flash earlier on cloudy than on clear days, i.e., that they respond to light of a specific intensity. Comparison of observation 8 with 9, and 10 with 11, indicates that at a given light intensity the fireflies begin to flash earlier in high than in low temperatures.

Figure 1 shows the results obtained if the light intensities recorded in Table I are grouped according to the dividing lines in the fourth column and the light intensities in each group are averaged together and plotted against the averages of the temperatures corresponding to each group, i.e., the light intensity at the time and place of first flash is plotted against the temperature at the same time and place. This figure shows that

temperature and light are interrelated factors in their effect on the time of the first flash, and that, for each degree of rise in temperature, flashing begins at a light intensity about 20 meter-candles more intense. Figure 1 indicates, in addition, that the time at which flashing begins depends primarily upon light and temperature and not upon the hour of day. However, the fact that in nature the fireflies do not flash again at dawn, even though conditions of light and temperature are the same as those under which they flash at dusk, shows that specific light intensity and temperature do not absolutely determine the time of day at which flashing occurs, and that the effect of a given light intensity appears to depend on whether it is reached by decrease from a higher intensity or increase from a lower.

In sum, these results indicate, in accordance with the observations of Allard and of Rau, that the flashing is correlated with light of a definite intensity, and, in accordance

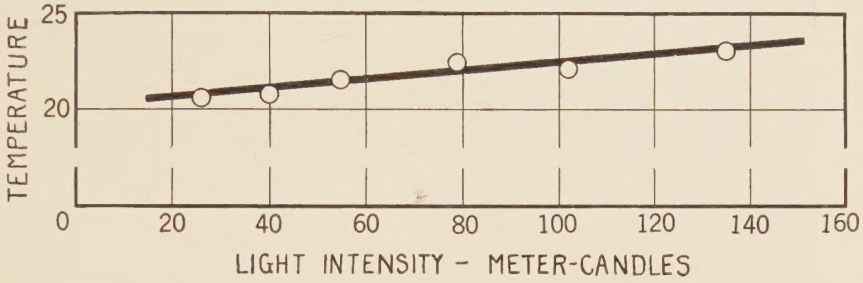

FIG. 1.—Relation between temperature and light intensity at the time of first flash. Graph constructed from the data presented in Table I, by plotting the averages of different groups of temperatures that obtained at the times of the first flashes on different evenings against the averages of the corresponding light intensities. Note the linear relation between temperature and light intensity.

with the observations of Mast, that temperature also has an effect on flashing. However, they offer little in support of the view that flashing is correlated with an inherent periodicity in the organism.

OBSERVATIONS IN THE LABORATORY

APPARATUS AND METHODS

In order to obtain more accurate information concerning the relation between flashing and light intensity than was obtained in observations in the field, an apparatus was constructed in a darkroom, with which it was possible to expose large numbers of fireflies to light of various fairly uniform intensities and to measure accurately the frequency of flashing under different controlled conditions. The apparatus (Fig. 2) consisted essentially of a floodlight (*F*), suspended on pulleys 3 meters above the floor of the darkroom, and a cage (*C*), made of mosquito netting, in which the fireflies were kept during experimentation. The cage was 2.5 m. long, 2 m. wide, and 0.6 m. high. The floodlight consisted of a battery of fifteen 200-watt frosted lamps with tinned 60° conical reflectors (*R*) 25 cm. in basal diameter, fastened to a wooden platform (*P*) 2 m. long and 1 m. wide. Different light intensities were obtained by varying the number of lamps turned on and by placing various cloth screens (*S*), 2×1.2 m., below the lamps on brackets (*B*).

With all the lamps turned on and no screens under them, the intensity of the light was 3,600 meter-candles in the middle of the top of the cage and 1,180 m.c. in the corners at the floor. For the sake of convenience this range of intensity is referred to hereinafter

as 2,500±m.c., which value represents the average intensity of the light in the cage under the conditions described above. With seven alternate lamps turned on and three screens under them, the intensity was 96 m.c. at the top of the cage and 48 m.c. in the corners at the floor. This range is referred to hereinafter as 65±m.c.

The temperature of the darkroom varied between 24° and 25° C.

The procedure in most of the experiments was in general as follows: Males of *P. pyralis* were collected in the field between 7:00 and 8:00 P.M. and put into quart milk bottles, twenty-five in each bottle. A little grass was added to each bottle to maintain favorable humidity. Promptly at 8:00 P.M. the bottles were completely covered with opaque

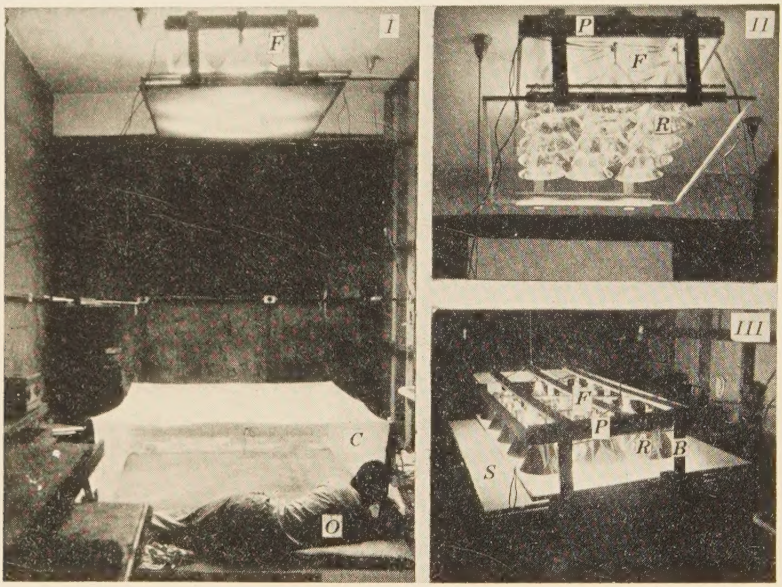

FIG. 2.—Photographs of apparatus used in darkroom to subject fireflies to light of various intensities. *I*, entire apparatus viewed from one end; *II*, lighting unit viewed from below; *III*, lighting unit viewed from above; *F*, floodlight; *C*, cage made of mosquito netting (2.5×2×0.6 m.); *P*, wooden platform (2×1 m.); *R*, conical tinned reflector; *S*, cloth screen; *B*, bracket for holding screens; *O*, observer.

black paper and taken into the laboratory. Here the fireflies were left in darkness for various lengths of time and then put into the cage (twenty-five at a time, i.e., the contents of one bottle) and exposed to various intensities of light and to various changes in illumination. They were closely observed under all of these conditions, and the total number of flashes per minute per twenty-five individuals ("frequency of flashing"[3]) was recorded. The results obtained are presented below.

THE EFFECT OF BRIGHT LIGHT ON FLASHING

In the laboratory different groups of fireflies were exposed to 2,500±m.c. for periods ranging up to 12 hours, to 800±m.c. for periods ranging up to 18 hours, and to 320±m.c.

[3] In most of the figures, for the sake of simplicity, the frequency of flashing is plotted as the average numbers of flashes per minute per twenty-five individuals in successive 5-minute periods, instead of as the actual numbers per minute.

for considerable periods of time. No flashing was observed in these intensities. In addition, fireflies which were flashing in dim light or in darkness were exposed to bright light, and it was found that all flashing ceased immediately. It is consequently concluded that bright light prevents flashing. The lower limit of intensity which prevents flashing was not precisely ascertained, but it is between 320 and 210 m.c. under ordinary conditions.[4]

THE EFFECT OF DARKNESS ON FLASHING

Effect of darkness following bright light.—Fireflies were subjected to darkness for various periods, then exposed in the cage to bright light (2,500±m.c.) for 15 minutes, and then subjected to darkness again (i.e., previous time in darkness varied, time in bright light constant). Figure 3 presents the results of several experiments of this type. This

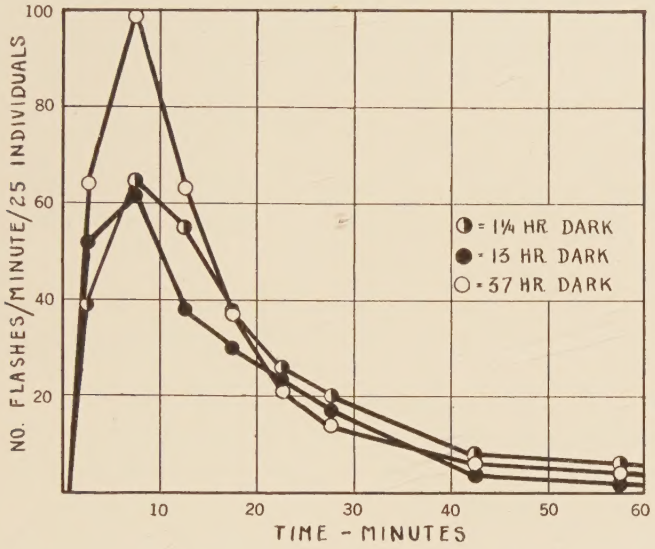

FIG. 3.—Relation between flash frequency and time in darkness preceding exposure to bright light. Fireflies were subjected to darkness for $1\frac{1}{4}$ hours (five experiments), 13 hours (two experiments), and 37 hours (two experiments), then to bright light for 15 minutes, then to darkness again, in which the frequencies of flashing were measured. Ordinates, average numbers of flashes per minute per twenty-five individuals.

figure shows that, when fireflies were exposed to bright light for 15 minutes and then subjected to darkness, the frequency of flashing increased precipitously to a maximum in about 8 minutes, then decreased rapidly for about 15 minutes, and thereafter decreased more gradually nearly to zero at the end of an hour. It shows also that the frequency of flashing in darkness following 15 minutes' exposure to bright light was greater if the fireflies had been previously subjected to darkness for 37 hours than it was if they had been subjected to darkness for 13 hours or for $1\frac{1}{4}$ hours.

[4] The fact that the fireflies ordinarily do not flash in the field during the day (intensities up to 100,000 m.c.) shows that there can be enormous variation in light intensity without flashing. Harvey (1926) reported that flashing in *Photuris pennsylvanica* was inhibited by exposure to 15,000 foot candles (160,000 m.c.) if the luminous organ alone was illuminated, but not if the eyes were illuminated while keeping the luminous organ in the dark.

In another series of experiments groups of fireflies were subjected to darkness for a given time; then some of them were exposed to bright light for 15 minutes, some for 30 minutes, others for 1 hour, others for 2 hours, and still others for 4 hours, after which they were subjected to darkness again (i.e., previous time in darkness constant, time in bright light varied). In these experiments it was found that flashing occurred whenever the intensity was changed from bright light to darkness, but that no consistent difference in the frequency of flashing in darkness was observed following the different times of exposure to bright light.

Effect of darkness following dim light.—Fireflies were exposed to dim light (65±m.c.) and left until flashing became infrequent or ceased, and were then subjected to darkness.

TABLE II

EFFECT ON FREQUENCY OF FLASHING OF REDUCTION IN INTENSITY FROM DIM LIGHT TO DARKNESS

Note that increase in frequency resulted.

Experiment	Number of Flashes per Minute in Dim Light in 5 Consecutive Minutes Previous to Subjection to Darkness	Average Flashes per Minute in Darkness	Number of Flashes per Minute in Darkness Following Reduction in Intensity from Dim Light to Darkness	Average Flashes per Minute in Dim Light
1	8, 2, 3, 0, 4, ...	3	4, 3, 7, 19, 16, 14, ...	10
2	4, 10, 3, 2, 3, ...	4	15, 17, 23, 21, 24, ...	20
3	1, 2, 2, 0, 0, ...	1	18, 22, 30, 20, ...	22
4	3, 3, 4, 0, 5, ...	3	8, 17, 10, 27, 21, ...	17
5	0, 0, 0, 0, 0, ...	0	4, 21, 21, 21, 16, 24, 21, ...	18
6	0, 0, 0, 0, 0, ...	0	0, 2, 11, 13, 11, 14, ...	8
7	0, 0, 0, 0, 0, ...	0	13, 29, 34, 32, 36, 35, 33, 25, 30, 38, 23, 21, 19, 17, 18, 15, 11, 7, 10, 5, 5, 10, 4, ...	20

The frequency of flashing was measured for 5 consecutive minutes previous to the exposure to darkness, and also for various periods after the change. Table II contains the results of seven such experiments. This table shows that reduction in intensity from dim light to darkness at once produced a very marked increase in the frequency of flashing, and that the flashing continued only a short time (Table II, Exp. 7).

Additional experiments showed that the lower the intensity of the dim light, the smaller the increase in the frequency of flashing resulting from reduction in intensity from it to darkness, and that exposure to darkness does not cause flashing in fireflies which have been in dim light for a considerable time without flashing.

Effect of continuous darkness.—Fireflies were brought in from the field in the evening in bottles, as described. Some of the bottles were unwrapped (not opened) in the darkroom in total darkness (three experiments); other bottles were emptied into the cage in total darkness (four experiments); one other was emptied into a large, covered glass

aquarium. In each of these eight experiments the number of flashes produced by the 25 fireflies was recorded for 5 consecutive minutes every half-hour or hour for 28 consecutive hours. The average of the results of these experiments is presented in Figure 4. This figure shows that the frequency rose to a maximum of about 5 flashes per minute per twenty-five individuals at the end of a half-hour; then, in another hour, declined practically to zero. Figure 4 shows also that the frequency remained at this low level (only an occasional flash) for about 20 hours, after which it rose again to about 2 flashes per minute and, after 3 or 4 hours, decreased again to zero. The significance of the slight increase in frequency which occurred when the fireflies had been in darkness about 23 hours will be considered later.

Summary.—The results presented show that change from bright light to darkness induces flashing; that change from dim light to darkness temporarily increases the frequency of flashing; and that the frequency of flashing in continuous total darkness is relatively very low.

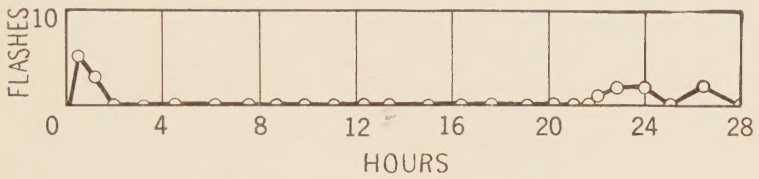

FIG. 4.—Frequency of flashing in continuous total darkness. Average of results of eight experiments. Ordinates, average numbers of flashes per minute per twenty-five individuals. Note that the frequency of flashing is relatively very low.

THE EFFECT OF DIM LIGHT ON FLASHING

Effect of dim light following bright light.—Fireflies were exposed to bright light (800± and 2,500±m.c.) for periods ranging from 15 minutes to 12 hours; then the intensity was reduced to that of dim light. In every test they immediately became active and flew about and flashed in an entirely normal manner regardless of the time of day. The fact that a sufficient reduction in intensity induces flashing at any hour of the day appears to support the contention of Rau that, in the field, flashing is correlated with definite light intensities; and it appears to offer no support to the view of Mast that the flashing is a periodic phenomenon.

Effect of dim light following darkness.—Bottles containing fireflies were taken into the laboratory, as described, and left in darkness for some time. Then the twenty-five fireflies from one of them were put into the cage and exposed to dim light (65±m.c.), and the frequency of flashing was recorded for an hour or more. Finally the fireflies in the cage were replaced by twenty-five from another bottle which had been in darkness longer, and the frequency was again measured. This general procedure was repeated with each group of fireflies.

Figure 5 presents the detailed results of three typical experiments. This figure shows that fireflies which were left in darkness for 1, 4, or 12 hours and then exposed to dim light began to flash almost at once, and that the frequency of flashing increased most rapidly and rose highest after 1 hour, and least after 12 hours, in darkness.

Figure 6 shows the results of forty-three experiments (similar to the three described above) in each of which the frequency of flashing in dim light was measured following

one of fifteen different periods in darkness. In this figure each point represents the average number of flashes per minute per twenty-five individuals for all the experiments performed with a particular period of subjection to darkness. Figure 6 shows the following: The frequency of flashing in dim light following, respectively, 1, 2, and 4 hours in darkness did not differ greatly, averaging about 45 flashes per minute; but thereafter it decreased markedly to about 11 flashes per minute following 8 hours in darkness, 3 flashes per minute following 12 hours in darkness, and practically to zero following 18 hours. After 24 hours in darkness the frequency was extraordinarily high, compared with the frequencies following 8, 12, and 18 hours. After 36 hours in darkness the frequency was low; after 48 hours it was high; after 60 hours it was low; after 72 hours, high; after 84 hours, low; after 96 hours, high. Each period of high frequency occurred approximately at 8:00 P.M.

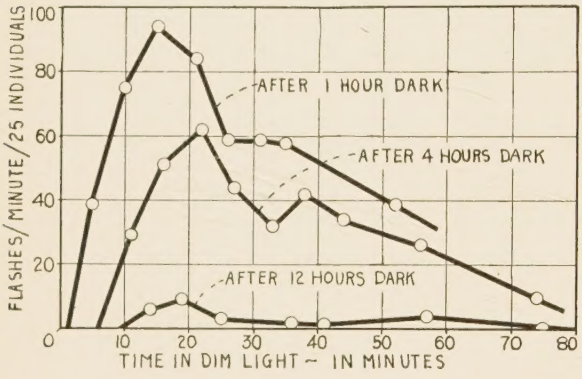

FIG. 5.—Frequency of flashing in dim light following various periods in darkness. Ordinates, average numbers of flashes per minute per 25 individuals.

These results show that, as the time in darkness previous to subjection to dim light increases, the frequency of flashing follows a definite cycle, in which periods of great flashing activity occur at 24-hour intervals, and that these periods alternate with periods of inactivity. Since the conditions in the darkroom under which the fireflies flash (following, e.g., 24 and 48 hours in darkness) are apparently precisely the same as those under which they do not flash (following, e.g., 36 and 60 hours in darkness), these results indicate that there actually is, as Mast maintained, an inherent diurnal periodicity in the flashing of these fireflies and that this periodicity persists for at least 4 days under the constant conditions of the darkroom. However, the fact that in the experiments described the periods of high frequency all occurred at about 8:00 P.M., as they do in the field, suggested that the periodicity might have been correlated with some unknown daily periodic change in the environment (e.g., cosmic rays) rather than with inherent periodic changes within the firefly. The results obtained in the following experiments concern this possibility.

Fireflies brought from the field at 8:00 P.M., as usual, were exposed immediately to bright light (2,500±m.c.) and left 12 hours (i.e., until 8:00 A.M.); then some were subjected to darkness for 12 hours (three experiments), and others for 24 hours (two experiments), after which they were exposed to dim light. Those which had been in darkness for 12 hours did not flash when exposed to dim light, although it was then 8:00 P.M.; but those which had been in darkness for 24 hours flashed vigorously, although it was then 8:00 A.M. The whole cycle had thus been reversed with respect to the time of day. In another similar series of experiments fireflies were exposed to 18 hours of bright light followed by 12 and 24 hours of darkness and then dim light. Again, those which had been in darkness 12 hours (i.e., until 2:00 A.M.) did not flash when exposed to dim light; whereas those which had been in darkness 24 hours flashed at once.

The results of these experiments show that the 24-hour cycle of activity can begin at any time of day, and consequently that it is not correlated with any periodic environmental change. It must, therefore, be correlated with a rhythm, inherent in the firefly, which under appropriate conditions persists regardless of the time of day. Confirmatory evidence concerning this conclusion is presented in the following paragraphs.

Effect of continuous dim light.—In the experiments thus far described concerning periodicity (e.g., Fig. 6), the flashing occurred in response to a *change* in light intensity from darkness to dim light. The question now arises as to what occurs in continuous illumination, or, in other words, whether or not the fireflies ever begin to flash of their own accord without any change in illumination.

Several groups of fireflies were brought from the field at 8:00 P.M., subjected to darkness, and left there, some for 1 hour, some for 12 hours, others for 36, others for 60, and

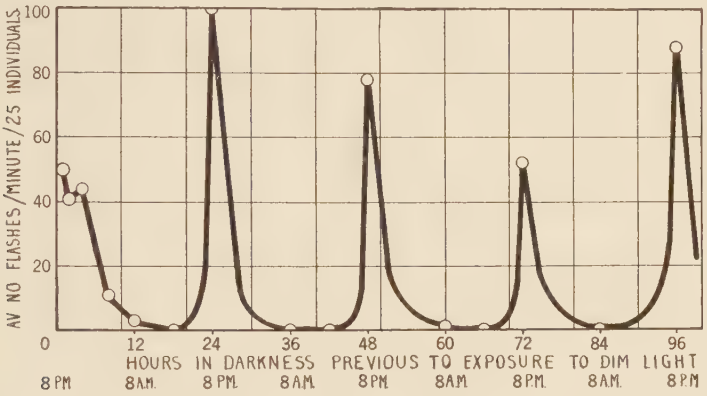

FIG. 6.—Frequency of flashing in dim light following various periods in darkness. Ordinates, average numbers of flashes per minute per twenty-five individuals in first 30 minutes of each experiment. Each point represents the average of several experiments, as follows: 1 hour, 2 experiments; 2 hours, 4; 4 hours, 5; 8 hours, 1; 12 hours, 5; 18 hours, 1; 24 hours, 2; 36 hours, 8; 48 hours, 1; 60 hours, 5; 72 hours, 1; 84 hours, 3; 96 hours, 1. Note the cycles of activity in which periods of high flash frequency recur at 24-hour intervals.

still others for 84 hours. Then they were exposed to dim light and left for 12 or more hours continuously, during which time the frequency of flashing was measured and recorded at regular intervals. Figure 7 illustrates the result of an experiment in which fireflies were exposed to dim light following 1 hour in darkness, and the frequency of flashing measured for more than 26 hours. This figure shows that the twenty-five fireflies exposed to dim light at about 9:00 P.M. flashed for 2 or 3 hours at a frequency of about 20 flashes per minute; then stopped and did not flash again throughout the rest of the night and the entire next day; but that at about 6:00 P.M. of the second evening they suddenly began to flash again spontaneously (i.e., without any change in light intensity), and that the frequency rose abruptly to over 120 flashes per minute and then decreased relatively rapidly nearly to zero.

Figure 8 shows the results of typical experiments in which the frequencies of flashing in dim light were measured following, respectively, 1, 12, 36, 60, and 84 hours in darkness. These curves show that following 12, 36, 60, and 84 hours in darkness the frequency of flashing in dim light remained practically at zero for about 12 hours and then

suddenly, without any change in the environment, increased enormously at approximately 24, 48, 72, and 96 hours, respectively, after the beginning of the experiments.

The results presented in Figures 7 and 8 confirm the conclusion previously reached that there is an inherent diurnal periodicity in the flashing, and show, in addition, that under appropriate conditions the periodicity is manifested by periods of flashing activity which occur at 24-hour intervals without any environmental change.

In a relatively small proportion of the experiments the expected recrudescence of flashing occurred prematurely, i.e., the flashing began earlier than would be expected if there is a 24-hour cycle. However, this did not occur in any of the experiments in which the fireflies were transferred to the cage from the bottles in total darkness several hours previous to the time at which they were exposed to dim light. The anomalous results were therefore probably due to mechanical stimulation of the fireflies caused by the transfer to the cage at the time they were exposed to dim light.

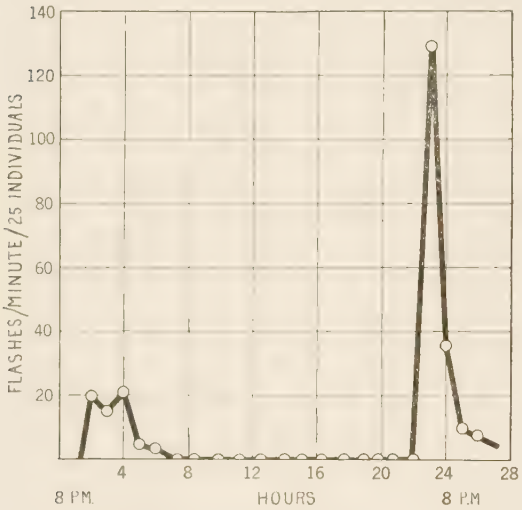

FIG. 7.—Frequency of flashing in continuous dim light following 1 hour in darkness. Frequency measured continuously for 26 hours. Note that a spontaneous recrudescence of flashing occurred after the fireflies had been in dim light for about 22 hours.

By referring to Figure 4, it will be seen that in continuous darkness there was a slight increase in flash frequency about 22 hours after the beginning of the experiments. The increase is too slight to be very significant, but the fact that it occurred in several experiments suggests that the 24-hour cycle persists to some extent even in total darkness.

THE EFFECTS OF SMALL CHANGES IN LIGHT INTENSITY ON FLASHING

Fireflies in the cage were exposed for some time to one of various intensities of dim light (3.2–130 m.c.); the frequency of flashing was recorded; and the intensity was then reduced or increased slightly and the frequency again recorded. The results obtained are presented in Table III, which shows that, between the limits of light intensity within which flashing occurs, reduction in intensity (Expts. 1, 5, 7) caused increase in frequency of flashing, whereas increase in intensity (Expts. 2, 3, 4, 6) caused decrease in flashing. This table shows also that there was no strict proportionality between the magnitude of the change in light intensity and the magnitude of the resulting change in frequency of flashing, although the general effects were unmistakable and in harmony with the conclusions already reached.[5]

MISCELLANEOUS INFLUENCES ON FLASHING

Temperature.—It has already been shown that temperature has an effect on the time of flashing. Snyder and Snyder (1920) found that increase in temperature resulted in

[5] It is interesting to note that whereas the intensity of full moolight is only about 0.24 m.c., the amount of flashing is very conspicuously less on moonlit nights than on moonless ones.

an increase in the frequency of flashing, and that flashing occurred only above 17° C. The writer confirmed these results.[6] However, since the same temperature may prevail at times when no flashing is occurring, as well as when flashing is occurring, it is obvious that flashing is not specifically correlated with temperature.

Humidity.—It was found that low humidity inhibits flashing through its injurious effect on the general vitality of the fireflies. For this reason the darkroom was artificially humidified during experiments involving more than a few hours' observations.

Experiments were performed to ascertain the effect of high humidity on flashing. Fireflies were placed in bottles in some of which the humidity was favorable and in

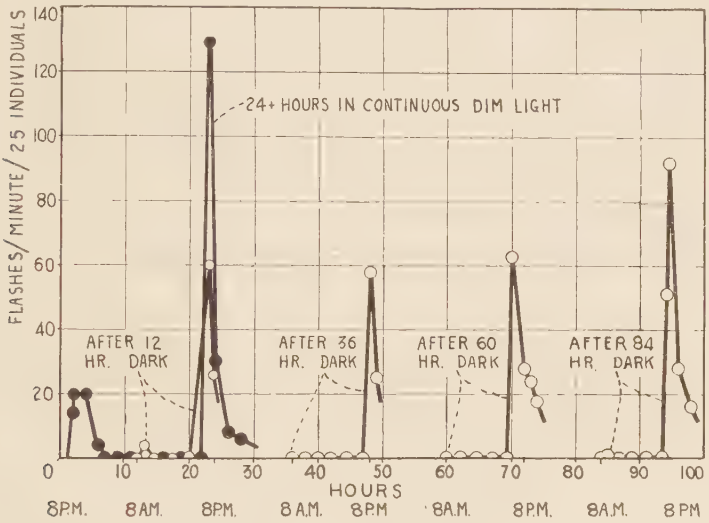

FIG. 8.—Frequency of flashing in continuous dim light following various periods in darkness. ●, exposed to dim light after 1 hour in darkness; ○, exposed to dim light after 12, 36, 60, and 84 hours in darkness. Number of experiments performed for each period of darkness: 1 hour, 1; 12 hours, 2; 36 hours, 7; 60 hours, 5; 84 hours, 1. Note the spontaneous bursts of flashing at about 24, 48, 72, and 96 hours after the beginning of the experiments.

others of which the air was saturated with water vapor (25°). The bottles were exposed to bright light for 75 minutes; then the fireflies were transferred to the cage, subjected to darkness, and the frequency of flashing was measured. The results obtained are presented in Figure 9, which shows that the fireflies which had been in very humid air flashed at a much lower frequency than those which had been in drier air. This depression in frequency was probably due to condensation of water vapor on the wings, which prevented flying and, secondarily, flashing.

Both low and high humidity thus decrease the frequency of flashing.

Air currents.—In the field it was often observed that wind affected the flashing of males in flight by blowing them off their course, causing a prolongation of the intervals between successive flashes (decreasing the frequency). In the laboratory, fireflies were exposed to dim light for some time, and their frequencies of flashing were measured. Then a gentle current of air (not strong enough to visibly interfere with flight) was caused

[6] Forthcoming publication.

TABLE III

EFFECT OF SMALL CHANGES IN LIGHT INTENSITY ON FREQUENCY OF FLASHING

The frequency of flashing is given as the number of flashes per minute per twenty-five individuals in consecutive minutes. Note that increase in intensity caused decrease in frequency of flashing, and vice versa.

Experiment	Change in Light Intensity (Meter-Candles)		Frequency of Flashing before Change	Average Frequency before Change	Frequency of Flashing after Change	Average Frequency after Change
	From	To				
1.....	27	10	5, 11, 16, 10, 3, ...	15	24, 22, 25, 24, 19, ...	23
2.....	10	27	8, 5, 9, 12, 6, ...	8	3, 4, 7, 2, 1, 0, 0, 1, 1, 4, 0, ...	2
3.....	65	130	4, 15, 5, 8, 10, ...	8	0, 0, 0, 0, 1, ...	0.2
4.....	27	54	18, 17, 18, 12, 18, ...	16	1, 4, 5, 4, 6, ...	4
5.....	54	27	20, 21, 16, ...	19	24, 22, 34, 37, 30, ...	29
6.....	3	14	2, 0, 2, 1, 5, ...	2	0, 0, 0, 0, 1, 0, ...	0.2
7.....	14	3	0, 0, 3, ...	1	12, 21, 18, 23, 27, ...	20

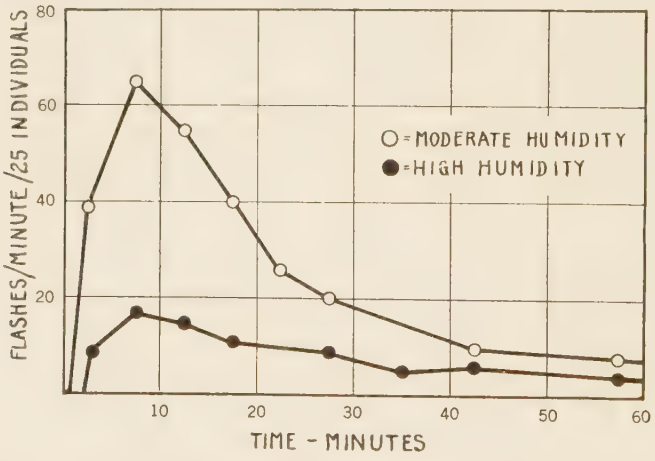

FIG. 9.—Effect of humidity on frequency of flashing. Upper curve, average frequency for five experiments in moderate humidity; lower curve, frequency in similar experiment in high humidity. Note that the high humidity decreased the frequency of flashing.

to circulate through the cage by means of an electric fan, and the frequency was again measured. The results obtained in three such experiments are presented in Table IV. This table shows that the current of air caused a considerable increase in the frequency of flashing.

TABLE IV

EFFECT OF AIR CURRENTS ON FLASHING

Frequency of flashing given as the number of flashes per minute per twenty-five individuals. Average lapse of 14 minutes between the time the ventilator was turned on and the time the frequency was measured again. Note that the currents of air resulted in increased frequency.

Experiment	Frequency of Flashing in Calm	Average Frequency in Calm	Frequency of Flashing Following Air Current	Average Frequency after Air Current
1.....	26, 22, 31, 30, 21, ...	26	57, 43, 46, 49, 47, 63, 48, ...	50
2.....	19, 18, 17, 12, 9, ...	15	37, 26, 36, 38, 19, 19, ...	29
3.....	0, 0, 1, 0, 0, 1, ...	0.3	8, 4, 0, 2, 4, ...	3

SUMMARY

1. Observations were made in the field by measuring various environmental factors and ascertaining their effects on flashing. Experiments were performed in the laboratory by subjecting fireflies to various changes in light and other agents and ascertaining their effects on flashing under controlled conditions.

2. In the field the time at which males of the firefly *P. pyralis* begin to flash is correlated with temperature and light intensity but not specifically with the time of day.

3. Bright light prevents flashing.

4. Change from bright light to darkness induces flashing; change from dim light to darkness causes a temporary increase in the frequency of flashing; the frequency of flashing in continuous total darkness is relatively very low.

5. Change from bright light to dim light induces flashing at any hour of the day, indicating that the response is correlated with a specific intensity of light.

6. Change from darkness to dim light induces flashing provided the fireflies have previously been in darkness for 24, 48, 72, or 96 hours, but not if they have been in darkness 12, 36, 60, or 84 hours.

7. Fireflies exposed to continuous dim light begin to flash spontaneously (i.e., without any environmental change) when the sum of the time spent in dim light and the time previously spent in darkness is equal approximately to 24 hours.

8. The periods of flashing activity which recur at 24-hour intervals may be made to occur at any hour of the day, showing that the periodicity in flashing is not correlated with any periodic change in the environment.

9. There exists in *P. pyralis* an inherent diurnal periodicity which is manifested by periods of flashing which recur at 24-hour intervals, and which persists for at least 4 days in the uniform conditions of the darkroom.

10. Between the limits of light intensity within which flashing occurs, reduction in

intensity results in increase in frequency of flashing, and increase in light intensity results in decrease in frequency of flashing.

11. The frequency of flashing is increased by increase in temperature and by gentle air currents, and decreased by high or low humidity.

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STUDIES ON THE FIREFLY. II. THE SIGNAL SYSTEM AND COLOR VISION IN PHOTINUS PYRALIS[1]

(One figure)

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A. The Signal System in *Photinus pyralis*

INTRODUCTION

THE mating habits of the firefly, *Photinus pyralis*, according to McDermott (1911) and Mast (1912), are essentially as follows: At dusk the male and female emerge from the grass. The male flies about, approximately 50 cm. above the ground, and emits a single short flash at regular intervals. The female climbs some slight eminence, such as a blade of grass, and perches there. She ordinarily does not fly at all, and she never flashes spontaneously, as does the male, but only in response to a flash of light, such as that produced by the male. If a male flashes within a radius of three or four meters of a female she usually responds, after a short interval, by flashing. "The male then turns directly toward her in his course and soon glows again. Following this the female again responds by glowing and the male again apparently takes his bearings, turns and directs his course toward her" (Mast, 1912, p. 260). This exchange of signals is repeated, usually not more than five or ten times, until the male reaches the female and mates with her.

Mast (1912) observed that males "seldom if ever" respond to the flashes of other males, and he therefore concluded that they somehow distinguish between the flashes produced by the female and those produced by other males. He listed (1912, p. 265) the following possible factors involved in this:

(1) The female is always at rest when she glows while the male is ordinarily on the wing; (2) the form of the luminous area differs in the two sexes; (3) there is always a certain time relation between the glow of the male and that of the female in response to it; (4) the quality of the light produced by the two sexes may differ; (5) the intensity may differ; (6) the duration of the glow may differ.

Mast maintains that he eliminated all these factors "save possible difference in the duration of the glow."

The question as to how the male distinguishes between the flashes of male and female was thus left unsettled. The present investigation was made in an attempt to answer this question. The first step taken was to measure accurately the time relations in the flashing signals.

[1] The writer wishes to express his gratitude to Professor S. O. Mast for kindly interest in the work and generous assistance in the preparation of the manuscript; to H. S. Barber, of the United States National Museum, for identifying the organism investigated; and to Master Samuel Damon for faithful assistance in the field.

EXPERIMENTAL

1. *The interval of time between successive flashes of males in flight.*—The intervals between successive flashes of males were measured as follows: A specimen flying about near by and flashing periodically was selected and closely observed. A stop watch was started each time the male flashed, and simultaneously a second stop watch was stopped, read, and reset. The results were dictated to an assistant, who recorded them. This was repeated with many individuals under various conditions, and in observations on some individuals as many as seventy consecutive intervals were measured. The results obtained are presented in Table 1.

TABLE 1*

THE INTERVAL OF TIME BETWEEN SUCCESSIVE FLASHES IN FREE FLYING MALES

Date (1933)	Temp. (C.)	Number of Individuals Studied	Total Number of Measurements	Mean Interval between Successive Flashes (Sec.)	Average Deviation from Mean (Total for All Individuals) (Sec.)	Per Cent Deviation from Mean (Total for All Individuals)
7/13	21.7	9	45	7.77	.85	10.90
7/9	22.8	4	33	6.00	.46	7.67
6/23	23.3	16	124	6.21	.37	5.97
6/24	23.3	12	177	6.10	.52	8.53
7/10	23.3	10	116	5.75	.42	7.30
7/6	26.1	7	60	5.67	.72	12.70
6/22	26.7	26	104	4.91	.42	8.57
7/20	26.7	11	63	5.21	.42	8.10
7/22	28.3	10	46	4.44	.41	9.20
General averages and totals	24.7	105	768	5.78	.51	8.77

* Each horizontal row represents the mean results for one evening.

Table 1 shows that on a given evening the intervals between successive flashes in a given male deviated, on the average, 8.77 per cent from the mean interval for the evening; that the mean interval of all those measured was about 5.8 seconds; that 90 per cent of the measurements fell within the limits 4.2–7.8 seconds, inclusive; and that the mean intervals on the different evenings differed considerably from one another, depending on the temperature.

The relation between temperature and frequency of flashing is shown graphically in the upper curve in Figure 1. This curve shows that the interval between flashes decreases as the temperature increases. The temperature coefficient (Q_{10}) from 23° to 29° C. is approximately 1.7, which value is in fair agreement with that (1.9) obtained by Snyder and Snyder (1920) in less extensive observations on an unidentified species.

2. *The interval of time between the flash of the male and the flash of the female in response to it.*—As noted by McDermott (1911) and Mast (1912), the female of *P. pyralis* responds readily to an artificial light under proper conditions, as well as to the flash of a male. The interval between the stimulus (flash of male or flashlight) and the response of the female is of the nature of a reaction time and will be called the "response interval" of

the female. The response intervals of twenty-three females responding to flashes produced by males, or by a flashlight were measured with a stop watch. The results obtained are presented in Table 2. This table shows that the response intervals of a given female varied, on the average, 5.67 per cent from their mean; that the mean response interval for all the measurements was 2.06 seconds; that 90 per cent of the measurements fell within the range 1.4-2.8 seconds, inclusive; and that the mean response interval differed somewhat in different females, depending on temperature.

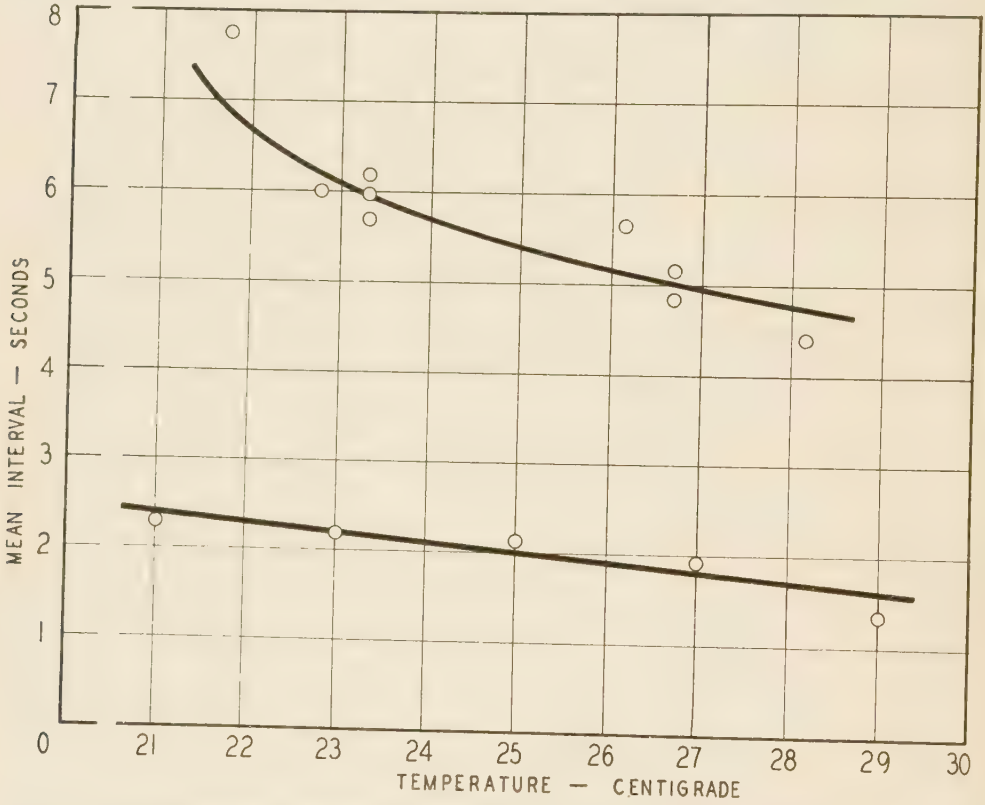

FIG. 1.—Relation between temperature and flashing in the firefly. Upper curve, each point represents the average interval between successive flashes of males on one evening, plotted against the temperature which obtained on that evening (data from Table 1); lower curve, each point represents the average length of the interval between the flashes of males, or of a flashlight, and the responses of females, over a range of 2° (data from Table 2).

The relation between response interval and temperature is shown in the lower curve in Figure 1. This curve shows that the length of the response interval of the female decreases with increase in temperature. The temperature coefficient (Q_{10}) for the response interval is approximately 1.5.

By comparing Tables 1 and 2 it will be seen that although the per cent deviations of the measurements of the response interval of the female are only slightly smaller than those of the measurements of the interval between successive flashes in the male, the

actual deviations are much smaller. The female, in fact, regulates her response interval with truly remarkable accuracy.

3. *Stimulation of the male by artificial light.*—The fact that the female invariably responds to the flash of the male after an interval of approximately 2 seconds suggested that the male might respond to an artificial light if it were flashed, like that of the female,

TABLE 2*

THE INTERVAL OF TIME BETWEEN THE FLASHES OF MALES OR OF A FLASHLIGHT AND THE FLASHES OF FEMALES IN RESPONSE

Date	Temp. (C.)	Number of Measurements on Same Female	Maximum Interval (Sec.)	Minimum Interval (Sec.)	Mean Interval (Sec.)	Average from Mean Deviation (Sec.)	Per Cent Deviation from Mean
7/27/33	21.0	20	2.7	1.9	2.17	.15	6.92
7/13/34	21.0	7	2.4	2.1	2.22	.09	4.23
7/13/34	21.0	16	2.5	2.1	2.32	.09	3.88
7/7/33	21.0	9	2.8	2.3	2.55	.17	6.67
7/5/33	22.3	10	2.8	2.7	2.78	.04	1.44
7/28/33	22.3	36	2.6	2.0	2.34	.12	5.13
7/18/33	23.0	27	2.6	1.9	2.31	.13	5.63
7/18/34	23.0	24	2.4	1.7	1.92	.13	6.77
7/16/34	24.0	28	2.7	2.2	2.37	.10	4.22
6/29/33	24.0	29	2.0	1.4	1.59	.12	7.56
7/18/33	24.4	22	2.7	2.1	2.38	.13	5.47
6/28/33	25.5	22	2.6	1.7	2.10	.16	7.62
7/29/33	25.5	40	2.1	1.2	1.51	.13	8.61
7/14/34	25.8	7	2.3	1.8	2.10	.12	5.72
7/14/34	25.8	13	2.4	1.9	2.21	.12	5.36
7/15/34	25.8	34	2.4	2.0	2.24	.10	4.39
7/19/34	26.0	9	2.5	1.6	2.16	.19	8.80
7/17/34	26.0	16	2.6	2.0	2.32	.12	5.20
7/19/34	26.0	31	2.4	2.0	2.16	.10	4.63
7/20/34	27.0	17	2.3	1.9	2.11	.12	5.68
7/20/34	27.0	9	2.0	1.6	1.76	.09	5.12
7/20/34	27.0	21	2.1	1.6	1.88	.11	5.86
7/30/33	29.4	33	1.6	1.1	1.35	.08	5.93
Averages and totals	24.5	480	2.4	1.8	2.06	.11	5.69

* Data divided into five groups, according to temperature, as averaged in plotting the lower curve in Figure 1.

2 seconds after his flash.[2] This experiment was performed by resting the end of a five-cell flashlight on the ground so that the light was directed into the grass at an angle,[3] and

[2] McDermott (1911) apparently used a similar system, flashing after "three to five" seconds, but he did not investigate the signals.

[3] Using this powerful flashlight, it was found that directing the light straight at the male did not usually elicit a response unless he was a long distance away, whereas he readily responded at any intermediate distance if not exposed to the direct rays of the flashlight. This shows that the male will not respond to light above a certain intensity. It was found, in addition, that a light intensity to which males responded

flashing it about 2 seconds after each flash of a male flying near by. The male turned and flew toward the flashlight in precisely the same manner that males respond to the flash of a female. The method was astonishingly successful, and it enabled the writer to exert an almost magical control over the male firefly. Individuals were "attracted" straight to the flashlight from distances of over 50 feet without difficulty, and fifteen or twenty males were often "attracted" to the flashlight at once (Buck, 1935).

4. *Orientation.*—A number of males were etherized, and, in each, one eye was completely painted over with opaque black enamel. It was found that these males gave no response whatever to flashes from a flashlight located on the blinded side, whereas they responded accurately to the same light when stimulated on the side of the functional eye. In the latter instance they flew toward the light sideward, keeping the functional eye oriented in the direction of motion. This experiment shows, first, that the response is certainly a visual one and not dependent on any sensitive tissue other than the eye, and, second, that orientation to light in the firefly is clearly not in accord with Loeb's theory of orientation in insects, which demands equal action of the light on symmetrically located receptors.

5. *The signal system.*—It was found that the male responds equally well to the flashlight whether the duration of the flash is 1 or $\frac{1}{50}$ second (estimated). This fact shows that Mast's conjecture that the male probably recognizes the flash of the female by reason of its being slightly different in duration from that of the male is not tenable.

It was found, in addition, that the male responds to the flashlight whether the area of the source of light is 1 square millimeter or 1 square decimeter; whether the flashlight is above, below, or to the side of the male, or moving either horizontally or vertically; whether the intensity of the light from the flashlight is very low or many times that of the light emitted by the female;[4] whether the color of the light is green, yellow, orange, or red.[5] These results confirm the conclusions of Mast that no possible difference in the color, intensity, relative motion of the light, or difference in the form of the luminous organ is of any importance in the discrimination between flashes produced by male and female. It was found, however, that males do not respond to flashes of artificial light under any circumstances unless they occur about 2 seconds after the flashes produced by the males. This strongly indicates that the response of the male depends upon the interval between his flash and that of the female.

Further evidence in support of this conclusion was obtained as follows: Males were "attracted" (one at a time) from some distance, and then, after they had approached to within less than 1 m. of the flashlight, the flashes were varied in diverse ways and the effects upon the responses of the males noted. The results obtained are summarized as follows: (1) two or three flashes in very rapid succession 2 seconds after the flash of the male—normal response; (2) flash at the same time as the flash of the male—no response;

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early in the evening often was too intense for use late in the evening. This indicates that what the male responds to is not so much the absolute intensity of the light as it is the difference between its intensity and that of the environmental illumination.

[4] From the average intensity of the light emitted by *P. pyralis* (1/100 candle; Coblentz, 1912) and the fact that males and females respond to one another at all distances between 1 cm. and 3 m., it is seen that in nature these fireflies respond to flashes of any illumination between 1/900 and 100 m.c., a relatively wide range. The precise limits of this range were not ascertained, but it was found in a previous study (Buck, 1937) that flashing is inhibited by intensities above about 210 m.c.

[5] Color vision will be treated in detail in sec. B.

(3) flash 1 or less seconds after the flash of the male—no response; (4) flash between 1.5 and 2.5 seconds after the flash of the male—usually response, depending somewhat on temperature; (5) flash 3 or more seconds after the flash of the male—no response.

As a crucial experiment a male was captured, held between thumb and forefinger, and gently pinched at intervals so that he emitted a flash approximately 2 seconds after each flash of a free flying male. The free male turned and flew to the captive male in precisely the same manner that males respond to a female or to an artificial light. This was repeated many times with different males, and the imitation of the female was so accurate that often the free male, after he had signaled with and approached the male held in the fingers, attempted to mate.

These results demonstrate conclusively that if there is any difference between the light emitted by the two sexes it has nothing to do with the ability of the male to distinguish between the flashes of the female and those of other males. They also make it practically certain that the discrimination by the male is dependent upon the regularity of the response interval of the female.

B. Color Vision in *Photinus pyralis*

INTRODUCTION

The term "color vision" is used in this paper in the sense commonly employed in insect physiology—meaning responses elicited by visual stimulation by lights of diverse wave-lengths. Bertholf (1931) and others have pointed out that the term is inapplicable in a strict sense to insects, because we do not know whether the subjective sensations of "color" are the same as in man.

The earlier literature on color vision in insects has been well reviewed by Graber (1883 and 1884) and Gross (1913), and the more recent by Imms (1931), Bertholf (1931), Eltringham (1933), and Mast (1936). The results presented show that in most insects color vision ranges roughly from 3500 to 6000 A, with the extreme limits extending perhaps as far as 2350 A in the ultraviolet and as far as 6770 A in the red.

METHODS

In the following experiments a flashlight and a series of "Wratten" light filters were used. In each test one of the filters was placed over the lens of the flashlight and covered light-tight with black paper in which a small hole was made in front of the filter.

In testing color vision in the female, a flash of the colored light transmitted by one of the filters was directed at her and the result noted. If she did not respond, the intensity of the light was changed by moving the flashlight nearer or farther away from her, or by using a more or a less intense source of light. If, in each of five consecutive tests, the female responded by flashing about 2 seconds after the flash of colored light, it was concluded that she saw the light.

In testing the male, a specimen on the wing was selected and illuminated by a flash of light transmitted by one of the filters, 2 seconds after each of his flashes. If the male responded to this treatment by turning toward the flashlight and flying to within 15 cm. of it from a distance of at least 3 m. it was concluded that he saw the light transmitted by the filter being tested.

Each filter was tested with many individuals of both sexes.

RESULTS

A summary of the results obtained is presented in Table 3. This table indicates that color vision in both sexes extends from some point between 5200 and 5600 A (in the green) to at least 6900 A (in the deep red), the latter being the longest wave-length yet recorded as visible to any insect.

The results obtained are perfectly trustworthy in the instances in which responses were obtained, that is, it is certain that color vision extends at least from 5600 to 6900 A (and almost certainly into the infrared, since the transmission of filter No. 88 is only 5 per cent at 7000 A), but the nonresponses are subject to some question because, as pointed out by Bertholf (1931), it is never possible to be certain that a nonresponse is due to the limit of vision's having been reached, or merely to the light's having been too weak.

TABLE 3*

RESPONSE OF *Photinus pyralis* TO LIGHT OF DIFFERENT WAVE-LENGTHS

"Wratten" Filter Number	Color	Range of Transmission in Visible Spectrum (Ångstroms)	Per Cent Transmission at Maximum Wave-Length in Visible Spectrum	Response
75	Blue-green	4700–5200	19 at 4900	No
58	Green	4800–6100	60 at 5200	Yes
74	Green	5100–5600	15 at 5300	Yes
22	Orange	5600–7000+	83 after 6400	Yes
72	Amber	5900–7000+	11.5 at 7000	Yes
29	Red	6100–7000+	69 after 6900	Yes
88	Infrared	6900–7000+	5 at 7000	Yes

* In the transmissions of the filters, values of less than 1 per cent are neglected. The results were the same in male and female.

The reason for believing that the lower limit of color vision lies somewhere above 5200 A is that whereas the fireflies responded readily to light transmitted by filter No. 58 at distances of 2 or 3 m., they did not respond to light transmitted by filter No. 75, even at a distance of 10 cm., representing a nine-hundred-fold increase in intensity. Calculation from the percentage transmissions of filter Nos. 58 and 75[6] and from the spectral energy emission data for the flashlight lamp used[7] shows that the total energy transmitted by filter No. 75 is about 12 per cent of that transmitted by No. 58. Nevertheless, since No. 75 proved ineffective even at intensities nine hundred times those which are effective with filter No. 58, it is concluded either that color vision does not extend as low as 5200 A or that the sensitivity of the eye of the firefly in the range of wave-lengths transmitted by filter No. 75 is less than one-one-hundredth of its value in the range transmitted by filter No. 58.

[6] *Wratten Light Filters* (10th ed.; Eastman Kodak Co., 1929). Pp. 86.

[7] The flashlight lamp used was Westinghouse No. 605, 13.9 lumens per watt, 6.0 volts, 0.5 amp., color temp. 2680° K. The author is indebted to Dr. C. S. Woodside, of the Westinghouse Laboratories, for the emission data.

SUMMARY

1. The male of the firefly *Photinus pyralis* flashes at fairly regular intervals, averaging 5.8 seconds. The length of the interval varies inversely with temperature.

2. The female of *P. pyralis* responds to the flash of the male by flashing approximately 2.1 seconds after his flash. The length of this response interval varies inversely with temperature.

3. The male is able to distinguish between flashes produced by the female and those produced by other males.

4. The male responds to flashes of artificial light and to flashes produced by other males if they occur about 2 seconds after his flash. This shows that no possible difference in the color, duration, or intensity of the light produced by the two sexes, or difference in the relative motion or form of the luminous area, is of any importance in enabling the male to distinguish between flashes emitted by male and female.

5. The essential factor in the ability of the male to distinguish between flashes produced by the female and those produced by other males is the fact that the female invariably responds to the flash of the male at a nearly constant interval of 2 seconds.

6. Color vision in both sexes of *P. pyralis* extends from some point between 5200 and 5600 A (in the green) at least as far as 6900 A (in the deep red), the latter being the longest wave-length of light yet recorded as being visible to any insect.

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